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## LX.—*A Contribution to the Morphology of the Limbs and Mouth-parts of Crustaceans and Insects.* By Dr. H. J. Hansen, of Copenhagen *.

It was chiefly in consequence of my work upon the Crustacea belonging to "Dijmphna-Togtet's zoolog.-botan. Udbytte" of 1884–1885 that I was led to the study of the morphology of the skeleton of this class of animals. Since then I have more than once devoted some time to similar morphological studies of most of the orders of all four classes of the Arthropoda, and it is my intention to publish a more extensive memoir dealing with a series of such questions in the case of the Insects, Myriopods, and Crustaceans. Many of the figures are already prepared; other circumstances have, however, induced me to resolve no longer to postpone a provisional publication of the greater portion of the most important of my results.

I may be permitted to mention that the views to be detailed in the following pages have been developed in the course of eight years as a result of the periodical investigations to which I have alluded; that I have been able to devote considerable time to repeated consideration, to the acquisition of a good supply of material, and to the practice of the necessary dissection, which is often very difficult owing to the small size of the majority of the objects, in order to make myself familiar

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with a large number of the animals, as also with the investigations and opinions of the anatomists, embryologists, and systematists with reference to the main details of the morphology and classification of the forms with which we are concerned. The greater part of these investigations have been carried out with the aid of the dissecting-microscope, often with a magnifying-power of one hundred diameters. My experiments show that it is often possible to study the articulation and composition of the mouth-parts much better with this instrument than by means of higher magnification under the compound microscope; the latter, however, is much more frequently employed. A reagent of which I have very often availed myself is a strong cold solution of caustic potash, in which the preparations are placed until the internal tissue is partially or completely decomposed and can be washed away in glycerine. I have frequently found it very advantageous to use specimens which had lain for a very long time in spirit so weak that the muscles and the connective tissue could be removed fairly easily by preparation, whereby I avoided the effect of the potash in making the thin chitin too transparent.

These observations are here made in case any one should wish to test or dispute my results, while at the same time I emphatically urge those who are interested in the subject to investigate in the manner indicated a larger series of forms belonging to several orders. Inducements for a test may possibly be afforded by my chief results, which are as follows:—The demonstration of three segments in the axis of the appendages of Crustacea as the primitive and still frequently existing condition; the division of the Malacostraca, based *inter alia* upon the different structure of the thoracic limbs; the demonstration of the existence in the case of Thysanura and certain Orthoptera of four pairs of mouth-parts, with which those of the Amphipoda are homologous; and the proof of a much greater agreement between the head of a *Machilis* and that of the malacostracous Crustacea than was hitherto assumed to be the case.

It would lead us too far afield to quote (not to speak of discussing) the enormous literature which belongs to the questions here indicated. Only once or twice do I refer to an author more precisely, when I have not found an opportunity of closely investigating the forms which are the subjects of his statements or am entirely ignorant of them; when, as most frequently happens, I content myself with giving the name of an author in parenthesis, it signifies that *the writer in question has expressed the same opinion before me* (thus affording a confirmation of my statement), *but that I*

*have myself also seen what is asserted*; besides this I have several times refrained from giving a quotation when it appeared to me to be entirely unnecessary or when an author could not be quoted without lengthy explanations. Certain of the statements alluded to are already to be found in my memoir in "Dijmphna-Togtet &c." (especially in the French *résumé* of the paper), and are there accompanied by figures; in "Cirolanidæ . . . . Musei Haun." some unimportant corrections are given.

## 1. GENERAL OBSERVATIONS.

1. It is probable that the appendages of the Crustacea primitively consist of an axial portion and two equivalent rami. On practical grounds, however, I employ the term endopodite for the axial portion and inner ramus, so that the outer ramus is considered as proceeding from one of the joints of the endopodite.

2. By comparison of the limbs of the Araneæ, *Thelyphonus*, Scorpiones, Chelonethi (*Chelifer—Obisium*), and Solifugæ we soon discover that the segments, with the exception of the two first, are not homologous one with another according to their parallel numbers (Gaubert). In order to determine the homology enumeration is not sufficient; we must in addition examine the form and length of the segments and especially the direction and form of the articulation. This conception, the correctness of which can easily be perceived in the case of Arachnida, is utilized in the case of the malacostracous Crustacea to deduce new results (§ 22).

3. If we would arrive at a comprehension of the mouth-parts and limbs of Insects, Myriopods, and Crustaceans from a really morphological point of view, we must first study them in different types belonging to the last-mentioned class.

4. In order to understand the structure of the maxillæ in the Malacostraca we must commence with the maxillipedes. For instance, in the case of the Isopods and Amphipods it is easy to see that the masticating-lobes, which arise from the inner side of the second segment or (in Gammarinæ) from the second or third segment, are simple processes starting from the inner angle of the respective segments; in *Eurycope*, for example, a lateral masticating-lobe of this kind is a simple prolongation, while in *Idothea entomon*, on the other hand, it is divided off by a secondary articulation which has a certain power of movement (*vide* "Dijmphna-Togtet," tab. xx.). Similarly the masticating-lobes of the two pairs of maxillæ must be regarded as processes from the sides of the several

segments of the endopodite of the jaw; in proportion to the segments these lateral processes often become extraordinarily large, greatly elongated, separated therefrom by an articulation, and even sometimes transversely divided, in consequence of which it is only with difficulty that they can be understood when but a superficial examination is made. It is therefore necessary to trace the segments in the endopodite of the maxillæ in thoroughly cleansed preparations, and at the same time to find out from which segment the chitinous lamellæ of the masticating-lobes proceed. This appears to me to be the only certain method of procedure, and, if this be done, all the secondary modifications of form &c. which take place in the masticating-lobes will no longer have a disturbing effect upon our conception of the morphology of the structures.

5. From reasons which the sequel will make readily intelligible I propose to term the first pair of jaws in Crustacea *maxillulæ* and the second pair maxillæ.

6. The *hypopharynx* (paragnathi, lower lip, tongue) in Crustacea has nothing to do with the appendages; it is a median and typically bilobed projection from the sternal portion of the head behind the mouth-opening.

## II. CRUSTACEA.

### a. ENTOMOSTRACA.

7. On examining the integument of the sixth appendage of an *Apus* (*Lepidurus productus* was the particular form I studied) after cleansing it with potash it is easy to see that it consists of six segments, each of which is provided with a lobe; in the case of the first five the lobes are articulated to their respective segments, while the sixth lobe is an immediate prolongation of the corresponding segment; the fourth and fifth segments, at least on the posterior side of the limb, are represented by distinct though small chitinous plates. On the anterior side of the limb it may be distinctly seen that the exopodite proceeds from the base of the third segment and the epipodite from the distal end of the second (*cf.* § 8), while the large first segment is devoid of a plate or outgrowth on the outer side. In the first pair of appendages the lobes of the third to the fifth segments have become very long and narrow and are divided into numerous small rings. In the eleventh pair of appendages in the female the external expansion of the endopodite forms one half and the exopodite the other half of the egg-sac; the epipodite is very small, although distinct.

8. In *Limnetis*, *Estheria*, &c. we find a similar structure; but in consequence of the delicacy of the integument of the appendages the difference between the chitin of the segments and the articulations is more or less indistinct. According to G. O. Sars, in *Cyclestheria Hislopi*: "The endopodite consists of six imperfectly defined segments, each of which is produced on the inner side as a rounded setiferous lobe . . . . the epipodite apparently issuing from the outer side of the second segment of the stem . . . . the exopodite originating immediately below the epipodite, from the outer side of the third segment of the endopodite."

9. Before the exopodite and epipodite, which are both present in *Branchipus*, there arises a very long and broad (partially cleft) plate on the outer side of the first segment. It has been shown by L. Lund (Nat. Tidsskr. ser. 3, 7 Bd., 1870) that a similar plate exists in *Cladocera*.

10. In the most highly developed Copepods, such as *Calanus*, the shaft of the second pair of antennæ is three-jointed (Kröyer) and in the mandibles the exopodite proceeds from the third segment, since after the actual mandible (first segment) there is found a small segment (described by Kröyer) which is usually overlooked. In the large *Metanauplius* stages I also succeeded in discovering three segments in the shaft of the second pair of antennæ and of the mandibles. In *Setella* the three segments in the shaft of the second pair of antennæ can be seen without difficulty.

11. In a series of large larvæ (*Metanauplius* stage) belonging to the family Calanidæ I have found antennules, antennæ, and mandibles, developed as in the *Nauplius*, and behind these five distinct but small pairs of plates, which are the rudiments of five pairs of appendages and of which only the two last show an indication of cleavage; these rudiments are consequently, to give them the designations applied by authors, maxillæ, first and second pairs of maxillipedes, and two pairs of swimming-feet. *There is some considerable distance between the points of origin of the rudiments of the first and second pairs of maxillipedes*, which are therefore entirely independent one of the other; indeed we even see on the dorsal surface and on the side of the animal a distinct articulation which extends across the ventral surface as a faint streak between the two rudiments. That my interpretation of these rudiments is correct is borne out by the fact that I possess specimens of the following stage, with all five pairs of appendages perfectly well developed, and only two of them are swimming-feet. I consider therefore that I am entitled definitely to conclude (indeed, according to Grobben,

the Calanidæ are "phylogenetically the oldest forms" among the Eucopepoda) that *the rudiments of the first and second pairs of maxillipedes arise entirely independently one of the other; consequently they each correspond to their own pair of appendages, and not to the outer and inner branches of one and the same pair.* Owing to the peculiarities in the structure and the relative position of the maxillæ and maxillipedes in the free-living and parasitic Copepods I regard the maxillæ as homologous with the maxillulæ, the first pair of maxillipedes as homologous with the maxillæ in the Malacostraca, and the second pair of maxillipedes as homologous with the maxillipedes (*e. g.* in the Amphipods), and, among other things, as exhibiting the same tendency towards mutual fusion.

12. In *Argulus* the swimming-feet consist very distinctly of a three-jointed shaft and two branches (Kröyer). The basal joint of the shaft is much shorter than the second and somewhat shorter than the third.

13. It follows from §§ 7–12 that *we must assume the presence of three segments in the stem of all cleft appendages in Crustacea to be a primary condition*; and this number has distinctly persisted, at any rate in the cases quoted.

## b. MALACOSTRACA.

### α. Leptostraca (§§ 14–17).

14. *Nebalia* must be assigned to the Malacostraca (Claus), and in many respects it approaches the Mysidæ, while the Euphausiidæ, on the contrary, are very far removed from it (*vide* § 26).

15. In *Nebalia bipes* the shaft of the second pair of antennæ consists not of three (Claus) but of five segments, and *the fifth segment shows a tendency to be composed of two* (Claus), which are well separated in *Nebaliopsis*; after removing the shield the first segment may be easily found by the aid of a good dissecting-microscope; this segment is somewhat short, but well marked off; the fourth segment is conspicuously marked off on the outer side, but is very short.

16. The limbs of the thorax consist not of seven but of *nine segments.* In *Nebalia bipes* we find on the outer side of the limb at the base a somewhat short but very distinct segment; after this there come the segments with the epipodite and exopodite, and finally the remainder of the limb shows three distinct incisions on the inner margin and three joints. (All these details are best seen in appendages laid

in water [not glycerine] and taken from large specimens which have been preserved for some time in fairly weak alcohol; they can, however, also be observed in ordinary glycerine preparations.) An examination of older preparations (most kindly lent to me by Prof. Claus) of *Paranebalia longipes*, W.-S., displayed no especially distinct conditions, yet in a pair of appendages I observed the small basal segment. In Sars's figure of the last pair of limbs this basal segment may be seen divided off on the outer margin ('Challenger' Report, vol. xix.); if we reckon two more segments for the epipodite and exopodite we get nine segments, since the figure alluded to shows beyond the base of the exopodite six segments, of which the last is very short (I have convinced myself of its existence in some legs from Claus's preparations).

17. The first segment of the maxillulæ bears a masticating-lobe of considerable size, which is articulated to it near the base; the second segment has only a narrow rigid plate of chitin and is destitute of the masticating-lobe; the third segment passes insensibly into a short broad lobe. These conditions can be very easily observed if the muscles are to a certain extent removed. (The composition of the maxillæ I have not been able to determine with certainty.)

## β. Eumalacostraca (§§ 18–27).

18. *Mysidæ*.—The antennæ have a six-jointed stem (cf. *Nebalia*, § 15); the outer ramus (squama) arises from the third segment (*cf.* Copepoda, § 10). The mandibles have a "*lacinia mobilis*" (for the explanation of this term see Hansen, "Cirolanidæ"). As in *Nebalia*, the two lobes of the maxillulæ spring from the first and third segments (*vide* "Dijmphna-Togtet"). The lobes of the maxillæ arise from the second and third segments (the boundary between the first and second segments is incorrectly indicated in "Dijmphna-Togtet") and *the exopodite from the third segment*. The first segment of the feet has disappeared, so that the exopodite springs from the second segment; the foot therefore consists of eight segments (*cf.* § 16), for I regard the claw as a modified segment, or, in other words, the terminal segment has become cheliform; the basal segment is much shorter than the second; the "knee," where the chief movement in a vertical direction takes place, is found between the fifth and sixth segments (Boas). In the earliest stages of the larva we find at the end of the abdomen two somewhat firmly chitinized, narrow, hard processes (van Beneden,

Nusbaum), *which must undoubtedly be homologous with the furca in* Nebalia; they are relatively of large size, especially in the penultimate larval stage, and are probably cast off in the penultimate ecdysis in the marsupium.

19. The Cumacea, Tanaidæ (which must be elevated into a separate order), Isopoda, and Amphipoda agree exactly in the structure of the mouth-parts (not including the suppression of the exopodite of the maxillæ, the suppression of the lacinia mobilis in isolated parasitic forms, and similar secondary reductions) and thoracic appendages with the Mysidæ in all the characters which are mentioned in § 18. It is very easy to study the structure of the maxillæ and maxillulæ in Amphipoda (*vide* "Dijmphna-Togtet") and Isopoda (*vide* "Cirolanidæ!"). In certain Isopods the stem of the antennæ is distinctly three-jointed, but in the majority of forms the first segment disappears and probably fuses with the head. Even where the so-called epimeres are strongly developed (as in certain Amphipods) the coxopodite (or the interval between the body and the articulation of the second segment) is always short and several times shorter than the basipodite.

20. In many Isopods the first segment of the six hindmost pairs of thoracic limbs is small and movable; in many other genera it develops as an "epimere," which, *e. g.* in *Idothea entomon*, is very large, marked off on the dorsal side by an arthrodial furrow, and on the ventral surface fused with the ventral ridge ("Bauchschiene"); but in *Idothea hectica* the upper arthrodial furrow has also disappeared and the "epimere" has certainly not been reduced to the point of disappearance, but has become fused with the segments of the body and forms larger or smaller portions of their sides (*cf.* §§ 24 and 49).

21. In certain Isopods (*Janira*) we find a large thorn upon the seventh segment of the thoracic appendages, articulated beneath the cheliform eighth segment, so that the foot is said to have two claws (*cf.* § 51).

22. The Euphausiidæ are a long way removed from the Mysidæ in consequence of a series of characters, certain of which only will be mentioned here. The stem of the antennæ is two-jointed; the mandibles have no lacinia mobilis. The limbs are composed of only seven segments (they are without the "claw"). The "knee" lies between the fourth and fifth segments; the first segment is almost equally as large as the second. I suppose the segments beyond the knee to be homologous with the sixth, seventh, and eighth (claw) segments in *Mysis*, and the fourth segment to be homologous

with the fourth and fifth segments of the Mysid limb taken together. I derive this conclusion from the development and direction of the articulations, and, moreover, I would point out that a precisely similar condition is found in the Pseudoscorpions: for, in the first two pairs of limbs in *Chiridium* (as I have proved with absolute certainty in Nat. Tidsskr. 3 R. Bd. xiv., and in a paper at present in the press) the femur is undivided; in *Chelifer* it is divided into a short "trochantin" and the true femur; while in *Garypus*, and still more in *Obisium*, the femur is differentiated into a long *pars basalis* and a short *pars tibialis**, so that it is impossible to determine the homology of the segments by means of numbers (*vide* § 2). The maxillulæ have lobes *on the first and third segments, and, in a certain larval stage, also on the third segment, an exopodite, which subsequently disappears; while the organ which in the adult animals is regarded as an exopodite by authors is a plate-like development of the first segment, which appears later on* †. The maxillæ as regards the origin of the lobes agree with the Mysidæ.

23. The Decapoda approach the Euphausiidæ very closely. The second segment of the maxillulæ is fused with the first, so that the lobes proceed from the first and second segments. The segmentation of the limbs is essentially the same as in Euphausiidæ (Boas), but it follows from § 22 that the names bestowed by H. Milne-Edwards upon the several segments cannot be employed without consideration in the case of the orders mentioned in § 19 according to the number of each segment, with the exception of the first three.

24. As shown in § 20, the coxopodite does not disappear in the Idotheidæ, but forms a portion of the lateral region of the body; *if we assume that the first segment of the limbs which has been described in the Phyllopoda*, but overlooked or misunderstood by the majority of authors, *likewise does not disappear, it consequently forms a larger or smaller portion of the pleuræ*. This view seems to be capable of explaining the fact that in the Decapods branchiæ are found both upon the pleuræ, upon the arthrodial membrane between the pleuræ and the limb, and also upon the coxopodite; since the portion of the pleuræ provided with branchiæ is to be regarded as originally belonging to the limb, so that we now find its vanished segment represented by branchiæ alone. Compare

* This latter condition must be regarded as the primitive one, and therefore a fusion of segments takes place; but for practical reasons I have employed the expressions used.

† *Vide* G. O. Sars ('Challenger' Report), who has figured this correctly, but given it a wrong interpretation; *vide* also "Dijmphna-Togtet."

with this the plate situated upon the outer side of this same first segment in *Branchipus* and Cladocera (§ 9), which probably subserves the purpose of respiration. In the same manner we may also explain the presence of the branchiæ arising from the body at the base of the limb in *Lophogaster*, *Gnathophausia*, and *Eucopia*.

25. According to §§ 22 and 18 the exopodite of the maxillulæ and maxillæ, if it is present at all, always proceeds from the third segment in the case of the orders mentioned; it therefore follows that in these two pairs of oral appendages the primitive number of segments in the stem of the appendages is preserved and that the first segment comes to belong to the same category as the mandible, but not the coxopodite of the limbs.

26. The Leptostraca are decidedly the lowest of the Malacostraca. The Mysidæ stand much nearer to them than do the Euphausiidæ in the structure of the second pair of antennæ (§§ 18 and 22), in the structure of the limbs, in the development of the larvæ, in the presence of the furcal rami in the earlier larval stages (§ 18), in the shape of the heart, and in the presence of a conical projection for the orifice of each vas deferens; they appear to me to be the lowest of the Eumalacostraca.

27. The old division into Thoracostraca and Arthrostraca strikes me as being quite untenable even when (with Grobben) we have excluded the Stomatopoda as being a section of equal value. The arrangement appears to me to be based altogether too much upon only two conditions—the presence of a shield and of stalked eyes, as opposed to absence of a shield and sessile eyes,—and, moreover, none of these characters is constant (Tanaidæ, Cumacea). I consider that the Eumalacostraca can be arranged much better in three divisions, of which the first will contain the Mysida, Cumacea, Isopoda, and Amphipoda, while the second comprises the Euphausiida and Decapoda. The first division possesses *a lacinia mobilis upon the mandibles; eight segments in the limbs, of which the last segment is cheliform and the first several times shorter than the second, while there are five segments before the knee; a marsupium; larvæ which are at first motionless and have a peculiar development; an elongated heart; shorter or longer processes for the orifices of the vasa deferentia; and no spermatophores*: while the second division is distinguished by having *mandibles without a lacinia mobilis; limbs composed of seven segments, of which the first is almost as well developed as the second, while before the knee there are only four segments, of which the fourth is certainly homologous with the*

*fourth plus the fifth in the case of the previous division; no marsupium; motile larvæ, which in the case of the lower forms have a* Nauplius *stage and a large series of ecdyses; a short heart; no processes for the orifices of the vasa deferentia;* and, lastly, *by the possession of spermatophores.* The third group is constituted by the Stomatopoda, which agree in some of their characters with the first and in others with the second division, but in various other respects occupy a very isolated position.

## III. INSECTA.

### *α.* Machilis (§§ 28–35).

28. The mandibles of *Machilis* are homologous with those of the Malacostraca; *in form they resemble those of the Cumacea, having a well-developed almost cylindrical pars molaris,* though they are without a lacinia mobilis; *in articulation and musculature they exhibit a surprising agreement with,* e. g., *Diastylis* and *Nebalia* (*vide also* § 37), *and herein diverge to the utmost extent from,* e. g., *Orthoptera and Coleoptera.*

29. The maxillæ are composed of three segments and an eight-jointed palpus. The basal segment (*cardo*) has no masticating-lobe; the second segment is produced into a long lobe, which is transversely segmented at the tip; the third segment is also produced into a lobe (*galea*) and the palpus arises from its outer side. *The structure of the maxillæ* (which may be very easily examined in a preparation which has been cleared with potash), *as regards the origin of the lobes from the second and third segments, consequently agrees precisely with that of the maxillæ of the Eumalacostraca, while, on the other hand, it is totally different from that of the maxillulæ.*

30. In the Isopoda (see a figure in "Cirolanidæ") and Amphipoda we find that the maxillipedes are situated very close together in the median line, and, moreover, in the latter order their first (or first and second) joints become fused together; the maxillæ are articulated in front and at some little distance from the median line, while the maxillulæ are attached somewhat further still from the median line, and the hypopharynx projects between and before their points of articulation; lastly, the mandibles are inserted far away from the median line, obliquely outside and above the maxillulæ and maxillæ. We meet with a similar arrangement of the mandibles, maxillæ, and labium in *Machilis* and, *e. g.*, also in the Orthoptera and Coleoptera.

31. *I regard the maxillæ in* Machilis (*vide* §§ 29, 32, and 39) *as decidedly homologous with the maxillæ* (*second pair of*

*maxillæ of authors) in the Malacostraca, and the labium as homologous with the maxillipedes and agreeing in many respects with these appendages in the case of the group mentioned.* The submentum is homologous with the first segment, which is fused in the Gammarinæ, and the mentum with the second segment, which in the Hyperinæ is likewise fused. At the tip of the mentum we find a segment, produced on each side into four lobes, which, as may be seen with sufficient clearness, belong to two lobes, each of which is cleft; and these I regard (among other reasons on account of a comparison with Orthoptera and Amphipoda, although I cannot bring forward any cogent proof derived from the skeletal parts) respectively as a lobe from the second segment (the innermost cleft lobe) and as the third segment of the labium with its cleft lobe: the palpus arises from the outer side of the third segment.

32. The hypopharynx is conspicuous, almost rectangular in shape, slightly emarginate in front, and homologous with the hypopharynx (paragnathi) in the Malacostraca. The organs which are termed "paraglossæ" by authors have nothing to do with the hypopharynx; in the skeleton of the head they are articulated at the bottom of the hypopharynx and have a somewhat complex structure, with an external process like a small single-jointed palpus, and towards the tip a distinct tendency to cleavage into two lobes. I regard these "paraglossæ" as homologous with the maxillulæ of Crustaceans (a supposition which is strengthened in the highest degree by their structure in *Japyx* and the Collembola, *vide* § 39); the essential difference in *Machilis* consists in the fact that they are situated somewhat nearer to the median line and lie partly in front of the hypopharynx; yet in *Argulus*, according to Claus, the maxillæ are enclosed together with the mandibles in the suctorial tube, and are consequently placed before the hypopharynx. (If a carcinologist should raise the objection that in the case of *Apseudes* we find a lobe resembling an appendage upon the hypopharynx, we must reply that in *Apseudes* only the elongated outermost anterior angles are segmented off in a secondary fashion, while in *Machilis*, *Japyx*, and the Collembola the maxillulæ arise from the skeleton of the head at the base of the hypopharynx, which in these animals is not cleft towards the tip.)

33. The thoracic appendages have an elongated coxa, which is attached to the body by means of a small and for the most part firmly chitinized segment, which is freely movable, and which on account of its position and shape we must regard as the first joint of the leg. I regard it as homo-

logous with the coxopodite in the Malacostraca (it resembles the first segment of the leg of a *Mysis*, but is, however, somewhat longer); the coxa therefore becomes homologous with the basipodite. To the outer side of the coxæ of the second and third pairs of legs there is articulated a conspicuous hairy "style," which is perhaps homologous with the exopodite (Wood-Mason).

34. The abdomen consists of eleven segments (ten + the telson), a number which is met with again in the Cicadaria, *Ephemera*-larvæ, and other forms; according to Lacaze-Duthiers it is the primitive number in the Insecta. The well-known styles on the underside of most of the segments are without doubt portions of rudimentary appendages, and we may perhaps, on account of their position and agreement in form with the styles of the thoracic legs, regard them as exopodites (Wood-Mason). The triangular plates which bear the styles, and from which the hindmost in particular, especially in the case of specimens which are scarcely half-grown, project backwards as somewhat large processes, I consider with tolerable certainty to be homologous with the stems of crustacean appendages (Wood-Mason). The styles of the tenth segment constitute the well-known "cerci," which are homologous with the cerci in other Insects.

35. In the Mysidæ and Amphipoda we find, as is well known, four pairs of mouth-parts, and behind these fourteen segments, of which the last is without appendages. I have shown above that in the case of *Machilis* the corresponding four pairs of oral appendages exist, and behind them we also find fourteen segments, the last of which is likewise devoid of appendages. The tendency, which in the Malacostraca is of frequent occurrence, to develop the last pair of abdominal fect in a peculiar manner and to retain these, while the five preceding pairs undergo reduction (Mysidæ, Cumacea), is also met with in the case of *Machilis* and other Insects.

### β. Campodea, Japyx, Collembola (§§ 36–39).

36. In the formation of the head and the structure of the mouth-parts these three types are very closely allied. They are especially distinguished by the well-known peculiarity, that the mandibles and maxillæ, with the exception of their tips, "lie within the head." This has arisen in consequence of the fact that the integument behind their points of insertion has become folded forwards and around them, like a reduplicature which contains tissues; and on the underside of the head the edges of this reduplicature have become firmly united with the lateral margins of the labium, so that the

latter throughout almost the whole of its length is connected with the lateral wall of the head. Consequently the mandibles and maxillæ do not really lie within the head at all, but, as in the case of *Machilis*, are attached to the integument of its sides, which has here become thin and smooth; and since the articular region of the inner lobes of the maxillæ and labium has undergone elongation, we understand how the reduplicature can extend almost as far as the end of the labium. (The necessary investigation is difficult, since the integument on the inner side of the reduplicature and on the portion of the lateral wall of the head which is covered by the reduplicature is very thin.)

37. The musculature of the mandibles resembles that of the Crustacea even more than it resembles the musculature of *Machilis*. It is only necessary to compare Meinert's figure of *Japyx* with my figure of *Diastylis Goodsiri* in "Dijmphna-Togtet" (I have only reproduced the three largest muscles or their tendons), or with Sars's figure of *Diastylis sculpta*, to be struck by the astonishing agreement in the form and direction of the muscles and of the large median muscle-plate. The mandibles are without a pars molaris, but, on the other hand, we find in *Campodea* a small lacinia mobilis.

38. The maxillæ consist of a cardo and second segment, which (as in *Machilis*) is continued into a lobe exhibiting a transverse segmentation in the neighbourhood of the tip. On the other hand, the third segment and the palpus are entirely wanting. What is termed by authors the outer lobe and palpus is not connected with the maxillæ (see especially Stummer-Traunfels, "Vergleichende Untersuchungen über die Mundwerkzeuge der Thysanuren und Collembolen," Sitzungsber. k. Akad. Wiss., math.-naturw. Cl., c. Bd., iv. Heft, Wien, 1891, Taf. i. figs. 7, 10, 11) and does not belong to them, but is, on the contrary, united to the "paraglossæ" and to the underside of the skeleton of the head which is covered by the labium.

39. In *Japyx solifugus* the hypopharynx is short and rounded off; the firm chitin of the "paraglossæ" is articulated to the chitin of the head behind the base of the hypopharynx. The paraglossæ themselves lie in front of the latter and coalesce with it for a certain distance; each of these "secondary tongues" is on the outer side connected by means of firm chitin with the outer lobe alluded to in § 38, and with a distinct three-jointed palpus. This entire structure, which lies in front of the maxillæ, constitutes the conspicuous and, in their basal portions, somewhat abnormally constructed maxillulæ. The inner lobe is the "paraglossæ"; the other two portions become the outer lobe and palpus. In the

higher Collembola the hypopharynx is of large size and the maxillulæ have only an inner and an outer lobe ("paraglossæ" and palpus). Stummer-Traunfels furnishes us with a good *résumé* of the extremely divergent interpretations of these parts by different authors, such as Meinert, Lubbock (who terms the "paraglossæ" the "second maxilla"), and Tullberg (whose description is on the whole excellent and who possessed a keen eye for the difficulties in the interpretations given by the two previous writers). The maxillulæ are, as has been already stated, inserted before the maxillæ and behind the point of origin of the hypopharynx; they have nothing to do with the labium.

40. It appears to me that the facts detailed in §§ 28–32 and 36–39, when taken together, show the great agreement that exists between the mouth-parts of the primitive Insects named and those of the Malacostracous Crustacea and that they render evident the homologies which I have set up.

41. *Lepisma* stands, as regards the structure of the mouth-parts and the thoracic feet, between *Machilis* and the Orthoptera.

42. *Hemimerus talpoides*, Walk.*, is a genuine Orthopteron, and in the structure of its mouth-parts approaches very near to *Forficula*.

43. Orthoptera.—The muscles of the mandibles, *e. g.* in *Acridium*, exhibit conditions which are very divergent from those found in the Thysanura. By comparison with *Machilis* (§ 29) and by a process similar to that adopted in the case of the Isopoda it may be shown that the maxillæ, *e. g.* in *Forficula*, are composed of a first segment (cardo) without a lobe, a second (transversely divided) segment with the masticating-lobe, and a third (very obliquely cleft) segment with the galea, together with a palpus proceeding from the third segment; the second and third segments with their four parts together constitute the "stipes." (In the interpretation of the boundary between the lobe and the segment in the case of the second and third segments I have here on practical grounds not followed the certainly more correct interpretation employed in the case of the Crustacea, according to which the basal division alone is termed the segment; but the question has the less interest since it only turns upon the determination of the actual boundary between the segment and its lobe.) The hypopharynx is well developed; the maxillulæ are still present in various forms (*e. g.* Forficulidæ and larvæ of Ephemeridæ) as a lobe, which is attached to the skeleton at the base of the hypopharynx.

* A paper of mine on this animal is nearly ready for the press.

44. Coleoptera.—The mandibles, maxillæ, and labium agree with the utmost exactness with those of the Orthoptera in structure and relative position. A difference arises in consequence of the fact that the hypopharynx is either so much reduced in size as to disappear, or, as seems to me more probable, has become firmly attached to the inner side of the labium, which on the whole becomes pressed upwards against the underside of the head more closely than in the case of Orthoptera; many peculiarities (*e. g.* in *Melolontha*) point to the probability of the latter explanation. The maxillulæ are entirely wanting.

45. The hypopharynx is a freely projecting organ only in the Thysanura, Orthoptera, and Diptera; apparently we also find it in the Rhynchota as a short free point (Wedde, and my own observation in *Nepa*). It is often termed "tongue," which may well be admissible, but is not very happy. On the other hand, many authors frequently employ the term "tongue" in a very arbitrary and objectionable manner for portions of the labium; "paraglossæ," a term which should be entirely rejected, is used sometimes for portions of the labium, and at others for parts of the maxillulæ.

46. The antennæ in Insects are sometimes regarded as homologous with the antennules and sometimes as homologous with the antennæ in Crustaceans. As an argument in favour of the former supposition we have the fact that the antennæ of Insects, as also the antennules of Crustaceans, are innervated from the deuterocerebrum (Viallanes); the second theory is supported by two reasons. As has been demonstrated with respect to both classes by a series of authors, the rudiments of the antennæ are postoral in position both in Insects and in Crustaceans; it is true that a single author has stated the same thing with reference to the antennulæ, but this is certainly very much open to doubt. In the terrestrial Amphipods (*Orchestia*) the first pair of antennæ, the antennules, have become very short, and in the most characteristic land-Isopods (*Armadillidium, Armadillo, Tylos, Syspastus*) they have become extraordinarily small and are reduced even to the point of disappearance, while the second pair of antennæ are well developed.

47. Upon the mandibles of certain Coleoptera and larvæ of several species of Ephemeridæ I have found a well-developed lacinia mobilis.

48. How far the embryonic provisional lobes which have been found by different authors in several of the higher orders of Insects (and with respect to which Korschelt and Heider write on p. 793 of their text-book: "This lower-lip-forma-

tion may be best compared to the paragnathi of Crustacea, although a homologization with the latter structures may well appear to be out of the question") can belong to the maxillulæ is a question which must receive further elucidation from future embryological investigations.

49. In different Insects we can (with especial ease in all Cicadaria in the case of all legs, with exception of the last pair in Fulgoridæ) demonstrate the existence of a plate, which moves together with the coxa and which is decidedly homologous with the first segment in the legs of *Machilis* (§ 33); this plate, which is termed the trochantin, consequently becomes homologous with the coxopodite in the Malacostraca. It therefore does not belong to the same type of structure as the mandible and the cardo of the maxillæ (§§ 28, 29, and 25).

50. The trochanter in the legs of Insects, as is well known, often attaches itself closely to the femur, but is nevertheless not to be regarded as a portion of the latter which has been secondarily constricted off; on the contrary, it is to be considered as homologous with the ischiopodite of the Malacostracan limb.

51. With reference to the origin of the paired claws in Insects, I think that I may make the following statement:— In the Collembola we meet with a structure which agrees in the closest manner with the condition discussed in § 21 in the case of certain Isopods. We find that the leg ends with a short but well-developed and very freely movable segment, from the tip of which there proceeds a long and powerful claw (with a somewhat large cheliform process on each side), while to the underside of the segment another smaller claw is articulated. If we now start from my morphological interpretation in the case of the Mysidæ (§ 18) the short movable segment becomes the penultimate segment of the foot, the large claw the last segment, and the lower claw a large thorn (*vide* a good figure in Tullberg). In *Japyx solifugus* the lower claw has passed up on to the side of the movable segment, though scarcely to the same level as the large claw, and it is also somewhat smaller than the latter. The transition to the ordinary double claws now becomes very simple. I recommend the foot of a large *Acridium* for examination; the claws have here attained an equal size and proceed from a segment which is well developed, especially on the underside of the foot, and of which the lamelliform prolongation between the claws forms an empodium.

As an attentive perusal of the preceding pages will show,

the majority of the facts and interpretations which have been developed above are most intimately connected with a series of other, partly new and partly old, facts which have been adduced by other authors; so that it is impossible arbitrarily to dispute some of them without subjecting a series of others to renewed investigation in various orders.

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LXI.—*Descriptions of new Australian* Hesperiidæ. By W. F. Kirby, Assistant in Zoological Department, British Museum (Natural History).

The butterflies noticed in the present paper were sent with others to the British Museum for determination by Messrs. Anderson and Spry, who are engaged in the preparation of a work on Victorian butterflies. They wished those specimens which appeared to be new to be deposited in the British Museum on condition that they should be described at once and the names communicated to them. All the species were taken within the limits of the colony of Victoria. A species which appears to be identical with one described by Plötz has been added, as the descriptions of this author are not very accessible and are cast in a form which often renders them somewhat difficult to follow.

*Trapezites Andersoni.*

Exp. $1\frac{1}{6}$ inch.

*Male.*—Upperside golden brown, with a slight purplish shade towards the borders of the wings. Fringes unspotted, dark grey on the anterior wings, lighter on the hind wings. Anterior wings: a broad pale yellow blotch, with its outer end suddenly widened upwards, fills up the outer half of the cell; beyond this are the three usual whitish subcostal spots, and there are also two square whitish spots just below and beyond the cell, separated by the middle median nervule. Within the lowest commences a straight oblique raised line of black scales, extending to the inner margin. The base below the cell is clothed with dark golden hair nearly as far as this black line. Posterior wings thickly clothed with golden hair, except along the costa, for two thirds of their length, and towards the inner margin nearly to the anal angle.

Underside pinkish grey; anterior wings with the pale markings as above, the space between inclining to blackish;